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Three New Species of *Bathymodiolus* (Bivalvia: Mytilidae) from Hydrothermal Vents in the Lau Basin and the North Fiji Basin, Western Pacific, and the Snake Pit Area, Mid-Atlantic Ridge

by

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Abstract. Three new species of *Bathymodiolus* are described and compared with *Bathymodiolus thermophilus* Kenk & Wilson, 1985: *B.* ***brevior*** from the Lau Basin and the North Fiji Basin, *B.* ***elongatus*** from the North Fiji Basin, and *B.* ***puteoserpentis*** from the Snake Pit area, Mid-Atlantic Ridge.

INTRODUCTION

The genus *Bathymodiolus* Kenk & Wilson, 1985, first collected in 1977 at hydrothermal vents on the Galapagos rift spreading zone (East Pacific Rise system) (Corliss & Ballard, 1977; Corliss et al., 1979), has been considered monotypic, its type species being *B. thermophilus* Kenk & Wilson, 1985. Since 1975, several expeditions to sites with hydrothermal vents or cold seeps in the Atlantic and Pacific oceans have taken place, and large mussels have been found in the benthic communities of many of the visited localities.

Bathymodiolus thermophilus was subsequently collected on a hydrothermal vent field of the East Pacific Rise, at 13°N, in a depth of 2630 m during the French-American expeditions BIOCYATHERM (March 1982), BIOCYARISE (March 1984), and HYDRONAUT (November 1987) (Desbruyères et al., 1982; Kenk & Wilson, 1985; Fustec et al., 1987; Tunnicliffe, 1991); however, other species were soon discovered at sites in the Atlantic and the western Pacific.

In the Atlantic, *Bathymodiolus*-like mytilids are now known from the Florida Escarpment, (26°2′N, 84°55′W, 3266 m), a cold sulfide and methane-enriched groundwater seep (Turner & Lutz, 1984; Paull et al., 1984; Hecker, 1985; Turner, 1985; fig. 4B–D; Gage & Tyler, 1991: fig. 15.13); from the continental slope off Louisiana, an area with hydrocarbon seeps (27°41′N, 91°32′W, 600–700 m and 27°47,5′N, 91°15,5′W, 640 m) (Childress et al., 1986; Kennicutt et al., 1988; MacDonald et al., 1990), from the Barbados Accretionary Prism, a cold seep region in a subduction zone (10°00′–10°35′N, 57°50′–59°00′W, 1000–2200 m) (Jollivet et al., 1990; Gage & Tyler, 1991; recent samples from the MANON and DIAPISUB expeditions); and from the Mid-Atlantic Ridge at 37°N (1500 m) (Gustafson, personal communication). The mussels of the mid-Atlantic Ridge site and the two Gulf of Mexico sites are now under study by R. Turner (Museum of Comparative Zoology, Harvard University, Cambridge), R. Gustafson and R. Lutz (Institute of Marine and Coastal Sciences, Rutgers University of New Jersey); and the species from the Barbados Accretionary Prism by R. von Cosel and B. Métivier (Muséum National d'Histoire Naturelle, Paris, France).

Another *Bathymodiolus*-like species was collected in June

1988 by the French submersible *Nautile* during the HYDROSNAKE expedition to the "Snake Pit" area, a hydrothermal vent region on a slow-spreading part of the Mid-Atlantic Ridge (23°23'N, 44°56'W, 3480 m) (Desbruyères, 1989; Tunnicliffe, 1991; Segonzac, 1992:596; see also Mevel et al., 1989).

Most western Pacific hydrothermal sites were also found populated with mussels—the Okinawa Trough (Hessler & Lonsdale, 1991), the hydrothermal vents of the Mariana Trough at 3595–3666 m (Hessler & Lonsdale, 1991), and the Fiji and Lau Back Arc Basins (Desbruyères, 1989; Jollivet et al., 1989).

In 1989, numerous specimens of two species of large mussels were sampled by the submersible *Nautile* during the French BIOLAU cruise to the Lau Back Arc Basin and the joint French-Japanese STARMER II expedition to the Fiji Back Arc Basin. One of these species was found on all four explored sites: the "Vailili" hydrothermal vent field and the site "Hine Hina" (without smokers) on the Valufa ridge, Lau Basin, southeast of the Fiji Islands and the "White Lady" and "Mussel Valley" sites in the North Fiji Basin. The other species was encountered only on the latter two sites. In the North Fiji Basin, both species occur sympatrically. The German research vessel *Sonne* collected *Bathymodiolus*-like specimens in the Lau Back Arc Basin as well. However, from the hydrothermal fields on the Manus spreading center in the Manus Back Arc Basin (Bismarck Sea, Papua New Guinea), no hydrothermal vent mussels have yet been recorded (Tufar, 1990; Tufar & Jullmann, 1991).

In this paper, the two western Pacific species from the BIOLAU and STARMER expeditions and the Atlantic species from the HYDROSNAKE expedition are described and compared with *Bathymodiolus thermophilus.*

MATERIAL AND METHODS

Most of the studied material, as well as the reference material of *Bathymodiolus thermophilus,* was collected during the cruises BIOCYATHERM, BIOCYARISE, HYDRONAUT, HERO '92, HYDROSNAKE, BIOLAU, and STARMER II aboard the French research vessel *Nadir,* with the submersibles *Cyana* and *Nautile,* organized by IFREMER (Institut Français de Recherche pour l'Exploitation de la Mer). The collected material was sorted by the Centre National de Tri d'Océanographie Biologique (CENTOB), Brest. The material obtained by the R/V *Sonne* was borrowed from the Senckenberg Museum, Frankfurt. The measurements of length and height were taken according to Kenk & Wilson (1985:fig. 1). The bulk of the material is deposited in the Muséum National d'Histoire Naturelle, Paris, France; and material from the STARMER II expedition is also in the National Science Museum, Tokyo, Japan; paratypes were sent out to several major museums. The statistical analyses were carried out using STATVIEW 512 + TM.

Abbreviations used in the text: AMS—Australian Museum, Sydney, Australia; BMNH—British Museum (Natural History) (now: The Natural History Museum), London, U.K.; LACM—Los Angeles County Museum of Natural History, Los Angeles; MCZ—Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts; MNHN—Muséum National d'Histoire Naturelle, Paris, France; NMNZ—National Museum of New Zealand, Wellington, New Zealand; NSMT—National Science Museum, Tokyo, Japan; SMF—Natur-Museum und Forschungsinstitut Senckenberg, Frankfurt/M., Germany; USNM—National Museum of Natural History, Smithsonian Institution, Washington, D.C.; ZMB—Museum für Naturkunde (formerly: Zoologisches Museum) der Humboldt-Universität Berlin, Germany; spm.—specimen, specimens; sta.—sampling station.

SYSTEMATICS

Family MYTILIDAE

Subfamily BATHYMODIOLINAE Kenk & Wilson, 1985

Bathymodiolus ***brevior*** von Cosel, Métivier & Hashimoto, sp. nov.

(Figures 1–10, 26, 30–34, 37, 38)

Type material: Holotype, MNHN, BIOLAU expedition, Lau Basin, Vailili vent field: 4 paratypes, same locality, MNHN, dry shells; 4 paratypes, MNHN, as alcohol-preserved specimens; 4 other paratypes, 1 in NSMT, 1 in USNM, 1 in MCZ, 1 in SMF, all same locality, preserved in alcohol. Hine Hina hydrothermal field, BIOLAU expedition, dive BL 01, 22°32'S, 176°43'W, 1842 m, 13 May 1989, A. Dinet, observer: 23 paratypes, 8 in MNHN, 1 in NSMT, 1 in USNM, 2 in MCZ, 2 in LACM, 2 in AMS, 2 in NMNZ, 2 in BMNH, 1 in SMF, 2 in ZMB.

Type locality: Vailili vent field, Valufa Ridge, Lau Basin, 23°13'S, 176°38'W, 1750 m, BIOLAU, dive BL 12, P. Crassous, observer, 24 May 1989.

Description: Shell large, up to 140 mm long, rather thin but solid, modioliform-oval, somewhat variable in outline, inflated, equivalve, length/height ratio 1.6–2.2. Juvenile specimens shorter and more oval than adults (Figures 7, 10). Beaks subterminal, at one-seventh of total shell length. Anterior margin rather broadly rounded; ventral margin in juvenile, half-grown, and subadult specimens somewhat convex or straight; in large, fully grown specimens more or less concave. Postero-ventral margin broadly rounded, postero-dorsal margin slightly convex to almost straight; postero-dorsal corner narrowly rounded; ligament plate slightly arched. Exterior smooth, with well-developed, irregular growth lines, dull. Some specimens with very faint, broad radial undulations visible on postero-dorsal slope, bifurcating and thus somewhat reminiscent of the sculpture of *Brachidontes*. Umbo broad, somewhat flattened.

Shell without periostracum dull whitish; interior nacreous white.

Periostracum strong, dark brown, in umbonal region lighter brown, smooth, somewhat dull, with no periostracal hairs (however, byssal endplates of other specimens always scattered over valve).

Hinge without teeth, anterior hinge margin slightly protruding toward ventral. Ligament opisthodetic, strong, extending over whole postero-dorsal margin to postero-dorsal corner. Subligamental shell ridge faint from under umbos to middle of ligament, then becoming obsolete, under beaks visible only in ventral and not in lateral view (Figure 4). Anterior adductor scar long-oval, arched, situated in front of umbo. Posterior adductor scar rounded-trapezoid, united with posterior scar of posterior pedal and byssus retractor muscle. Anterior scar of same muscle separated and situated under ligament, at about two-thirds of its length (Figure 4). In juvenile specimens (up to 40–50 mm), scar located under end of ligament. Anterior byssus retractor muscle scar just under beak, on anterior part of umbonal cavity, visible only in posterior and ventral view but not in lateral view of interior. Pallial line ventrally only slightly concave or straight.

Larval shell 400 μm long and nearly 400 μm high. Separation present between very small protoconch I (about 100 μm long) and large protoconch II, which indicates a long planktonic larval phase (Figures 30–33).

Animal with large ctenidia which are slightly more than two-thirds shell length; outer and inner demibranch of nearly equal size. Inner mantle folds separate along whole ventral margin length from anterior adductor to posterior margin. Mantle folds on anterior end pass from ventrally over anterior adductor muscle up- and foreward along anterior margin, then fold down- and backward to pass again lower end of anterior adductor muscle toward ventral margin. Short, narrow, and rather strong and thick valvular siphonal membrane reaching from postero-ventral corner to siphonal opening, without papilla toward anterior margin (Figure 26, right). Foot thick, broad, and flattened, with ventral byssal groove two-thirds length of foot. Foot-byssus retractor muscle complex with anterior retractor moderately long; posterior byssus retractors consisting of two rather strong, diverging muscle bundles with common base at base of byssus. Anterior bundle short and broad, arising rather steeply toward attachment point on shell interior; posterior bundle longer and equally thick or thinner, passing at very low angle to longitudinal shell axis toward attachment point directly in front of posterior adductor. Posterior foot retractor well developed, arising from base of foot, well in front of base of byssus retractor muscles, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor; reaching inner shell surface closely appressed to anterior bundle over half to two-thirds its length. Labial palps narrow-triangular, anterior two slightly smaller than posterior pair.

Selected measurements (length, height, tumidity) with length–height ratios:

143.5 × 65.0 × 56.1 mm paratype MNHN	BL 12	2.2
140.1 × 63.9 × 57.6 mm paratype MNHN	BL 12	2.2
133.5 × 62.2 × 56.7 mm paratype MNHN	BL 12	2.1
132.5 × 67.5 × 60.5 mm holotype	BL 12	2.0
127.9 × 63.0 × 55.0 mm paratype MNHN	BL 12	2.0
127.5 × 61.3 × 52.5 mm paratype MNHN	BL 12	2.1
125.6 × 61.7 × 50.6 mm paratype MCZ	BL 12	2.0
125.3 × 59.8 × 56.4 mm paratype MNHN	BL 12	2.1
124.7 × 57.8 × 53.6 mm paratype MNHN	BL 12	2.15
112.8 × 53.8 × 50.9 mm paratype NSMT	BL 12	2.1
108.5 × 51.3 × 42.1 mm paratype USNM	BL 12	2.1
104.3 × 50.2 × 40.8 mm paratype MNHN	BL 01	2.1
104.1 × 52.7 × 42.4 mm paratype SMF	BL 12	2.0
103.8 × 53.5 × 39.3 mm paratype MNHN	BL 01	1.9
103.3 × 53.1 × 42.3 mm paratype AMS	BL 01	1.9
103.2 × 48.4 × 40.0 mm paratype SMF	BL 01	2.1
102.3 × 51.0 × 41.3 mm paratype LACM	BL 01	2.0
102.1 × 50.8 × 41.1 mm paratype NSMT	BL 01	2.0
101.6 × 50.5 × 42.7 mm paratype MNHN	BL 12	2.0
98.3 × 51.4 × 40.0 mm paratype USNM	BL 01	1.9
98.0 × 49.8 × 37.5 mm paratype NMNZ	BL 01	2.0
96.4 × 47.7 × 39.4 mm paratype ZMB	BL 01	2.0
93.8 × 48.5 × 38.2 mm paratype LACM	BL 01	1.9
90.2 × 47.7 × 36.4 mm paratype MNHN	BL 01	1.9
89.1 × 45.0 × 38.9 mm paratype MNHN	BL 12	2.0
88.4 × 45.3 × 37.3 mm paratype NMNZ	BL 01	2.0
86.2 × 42.0 × 34.8 mm paratype BMNH	BL 01	2.1
84.7 × 44.3 × 33.1 mm paratype BMNH	BL 01	1.9
84.1 × 40.3 × 33.3 mm paratype MNHN	BL 01	2.1
83.8 × 44.0 × 32.2 mm paratype ZMB	BL 01	1.9
81.5 × 44.1 × 33.1 mm paratype MNHN	BL 01	1.8
81.5 × 39.0 × 30.7 mm paratype AMS	BL 01	2.1
78.7 × 44.0 × 31.4 mm paratype MNHN	BL 01	1.8
74.0 × 39.8 × 31.1 mm paratype MCZ	BL 01	1.9
66.0 × 35.0 × 24.1 mm paratype MCZ	BL 01	1.9
62.1 × 36.1 × 25.0 mm paratype MNHN	BL 01	1.7
48.8 × 30.2 × 20.3 mm paratype MNHN	BL 01	1.6

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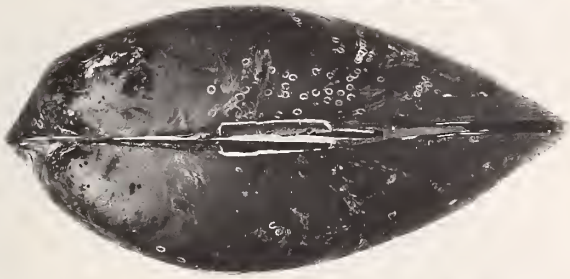
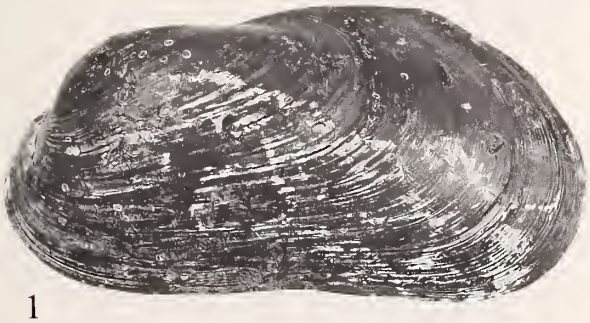
Explanation of Figures 1–5

Figures 1–5. *Bathymodiolus* ***brevior*** von Cosel, Métivier & Hashimoto, sp. nov. Figure 1. Holotype, MNHN, 132.5 mm. Vailili vent field, Lau Basin, 23°13′S, 176°38′W, 1750 m, BIOLAU, dive BL 12. Exterior and interior of right valve, dorsal view, exterior of left valve. Figure 2. Exceptionally bean-shaped specimen, 86.9 mm., perhaps another species, BIOLAU, dive BL 05. Ventral view of the animal showing foot with byssus and the large gills, and exterior of right valve. Figure 3. Specimen from Mussel Valley, 111.9 mm, STARMER II, dive PL 19. Exterior of left valve (see also Figure 8). Figure 4. Paratype, MNHN, 140.0 mm, BIOLAU, dive BL 12. Interior of right valve. The muscle impressions in this and most following interior of valve views are marked with pencil. Figure 5. Paratype MNHN, 103.6 mm, dive BL 1. Interior and exterior of left valve and ventral view to show the position of foot/byssus retractor muscle scars.





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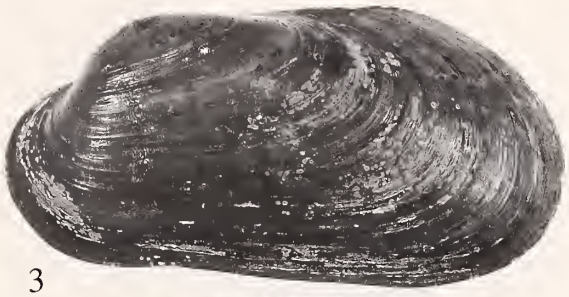

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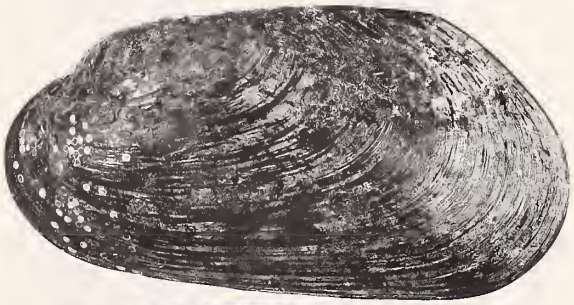

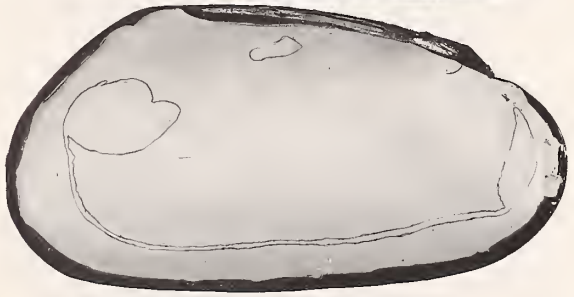

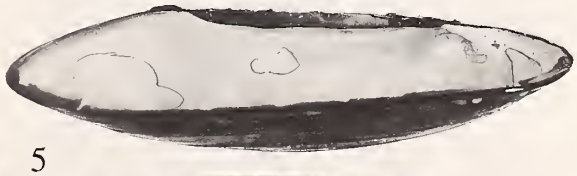

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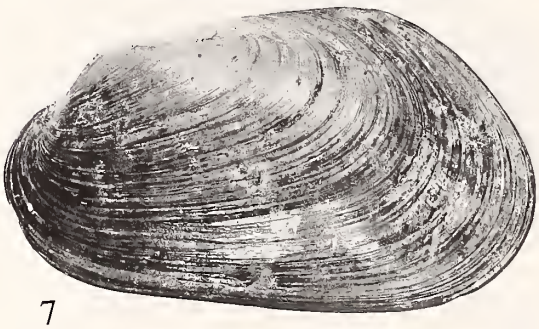

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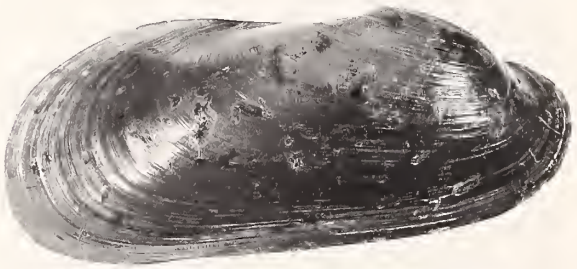

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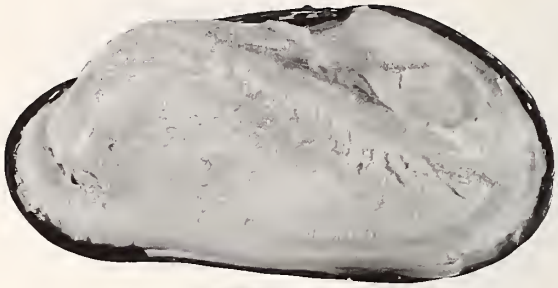

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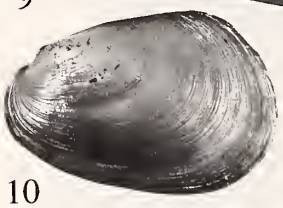

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Material examined: Type material; other material: Lau Basin, Vailili hydrothermal field (with smokers): BIOLAU dive BL 04, 23°13′S, 176°38′W, 1750 m, 16 May 1989, A. Dinet, observer, 12 spm.; BIOLAU dive BL 12, same locality, 24 May 1989, P. Crassous, observer, 3 spm. Hine Hina hydrothermal field (without smokers): BIOLAU dive BL 01, 22°32′S, 176°43′W, 1842 m, 13 May 1989, A. Dinet, observer, 40 spm.; BIOLAU dive BL 03, same locality, 1853 m, 15 May 1989, G. Barbier, observer, 106 spm.; BIOLAU dive BL 05, South of Hine Hina, 1885 m, 17 May 1989, A. Fiala, observer, 16 spm., all MNHN; 22°12,73′S, 176°36,43′W–22°13,06′S, 176°36,57′W, 1757–1703 m, dredged, R/V *Sonne,* cruise 67–2, sta. 183 GA, 26 spm., SMF. North Fiji Basin, White Lady hydrothermal field: STARMER II, dive PL 10, 16°59,5′S, 173°55,4′W, 2750 m, 5 spm.; STARMER II, dive PL 11, 16°59,5′S, 173°55,47′W, 2750 m, 5 spm.; STARMER II, dive PL 13, 16°59,5′S, 173°45,47′W, 2750 m, 4 spm.; STARMER II, dive PL 20, 16°59,5′S, 173°55,47′W, 2000 m, 24 spm.; Mussel Valley hydrothermal field: STARMER II, dive PL 19, 18°50′S, 173°29,0′W, 2750 m, 1 spm.

Habitat: The specimens live byssally attached to hard bottom around the hydrothermal vents; photos taken during the dives show dense clusters of mussels which are attached to each other in several layers. At the "White Lady" site, the mussels were grouped in a concentric ring around the vent where the water temperature was 3–4°C. Closer to the vent, the gastropods *Alviniconcha* (at temperatures of 10–20°C) and *Ifremeria* (at temperatures of 5–8°C) were found (Bouchet & Warén, 1991). The site is described in detail by Jollivet et al. (1989).

Distribution: Known from the North Fiji Basin and the Lau Basin, Fiji back arc.

Etymology: *brevior* (Latin) = shorter, referring to the difference in length/height ratio compared to the other mussel of the North Fiji Basin (see next description) and the working name "stout" given to this mussel.

Remarks: The major difference between *B.* ***brevior*** and *B. thermophilus* in the soft parts is the absence of fusion of the inner mantle folds along the anterior half of the ventral margin. The "valvular siphonal membrane" (Kenk & Wilson, 1985) along the posterior part of the ventral margin (which also results from fusion of the inner mantle folds) in *B. thermophilus* reaches nearly to the middle of the shell. It ends in a central marginal papilla, leaving a very small byssal-pedal gape between it and the anterior mantle fusion, whereas in *B.* ***brevior,*** the membrane is stronger and terminates at the postero-ventral corner, without a papilla. In *B.* ***brevior,*** the posterior bundle of the posterior byssus retractor is somewhat thinner, and the angle of divergence of both bundles larger than in *B. thermophilus.* (compared with fig. 5 of Kenk & Wilson, 1985). In *B.* ***brevior,*** the anterior retractor attaches more anteriorly.

The shell of *B.* ***brevior*** is somewhat stouter and more tumid than that of *B. thermophilus.* It has a broader anterior part and a longer dorsal margin and ligament; the umbo is placed slightly more posteriorly. The scar of the anterior part of the posterior byssus retractor muscle is situated more forward and at a greater distance from the scar of the posterior part of the byssus retractor muscle, which is united with the posterior adductor scar. Moreover, in *B. thermophilus,* it is situated under the end of the ligament, but in adult *B.* ***brevior*** at two-thirds of the ligament length. The ligament of the new species ends abruptly just in front of the postero-dorsal corner, whereas in *B. thermophilus,* it ends in a more or less pronounced taper. The subligamental shell ridge, which in *B. thermophilus* is prominent under the beaks, is rather weak throughout the ligament length in *B.* ***brevior*** and becomes obsolete toward the ligament end. The anterior byssus retractor scar in *B. thermophilus* is situated in the umbonal cavity behind the beak; in *B.* ***brevior,*** it is directly under the beak. The ventral pallial line of *B. thermophilus* is markedly deflected upward in its anterior part, whereas in *B.* ***brevior,*** it is nearly straight. The color of the periostracum in *B. thermophilus* tends toward olive-brown, whereas in most observed specimens of *B.* ***brevior,*** it tends toward mahogany.

The adult specimens of *B. thermophilus* from the Galapagos Rift vents figured by Kenk & Wilson (1985:figs. 2–3) are more or less arcuate, whereas the 13 examined specimens of that species from the East Pacific Rise (13°N), (maximum length: 152 mm) have a straight to only weakly concave ventral margin; their byssal-pedal opening is

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Explanation of Figures 6–12

Figures 6–10. *Bathymodiolus* ***brevior*** von Cosel, Métivier & Hashimoto, sp. nov. Figure 6. Juvenile specimen, 53.8 mm, BIOLAU, dive BL 03. Exterior and interior of right valve. Figure 7. Paratype MNHN, juvenile specimen, 78.8 mm, BIOLAU, dive BL 1. Exterior of left valve. A very short and high specimen. Figure 8. Specimen from Mussel Valley, 111.9 mm, STARMER II, dive PL 19. Ventral view, left valve removed. Note the polychaete worm in the pallial cavity (The two small sticks keep the mantle edges open) (see also Figures 3 and 26). Figure 9. Specimen with clear-colored periostracum, 89.8 mm, BIOLAU, dive BL. 05. Exterior of left valve. Figure 10. Juvenile specimen, 34.5 mm, BIOLAU, dive BL 03. Exterior of left valve. Figures 11–12. *Bathymodiolus* ***elongatus*** von Cosel, Métivier & Hashimoto, sp. nov. Figure 11. Holotype, MNHN, 140.6 mm, "Mussel Valley" site, North Fiji Basin, 18°50′S, 173°29′W, 2765 m, STARMER II dive PL 18. Exterior and interior of right valve. Figure 12. Paratype, MNHN, 115.9 mm, Same locality. Exterior of right valve and dorsal view.

somewhat larger than in the Galapagos Rift specimens as figured by Kenk & Wilson (1985:fig. 8). There are reported genetic differences between the Galapagos Rift and the 13°N populations (Grassle, 1985); nevertheless, they are here considered conspecific. A strongly bean-shaped mussel was taken during the BL 05 dive (Figure 2); this is considered an aberrant specimen of *B. **brevior***, but it might also represent another, still unnamed, species.

*Bathymodiolus **elongatus*** von Cosel, Métivier & Hashimoto, sp. nov.

(Figures 11–20, 25, 28, 35, 37, 38)

Type material: Holotype, MNHN, STARMER II expedition, "Mussel Valley" site; 17 paratypes, same locality, MNHN, preserved in alcohol; 18 other paratypes: 2 in NSMT, 2 in LACM, 2 in USNM, 2 in MCZ, 2 in AMS, 2 in NMNZ, 2 in BMNH, 2 in SMF, 2 in ZMB, all from same locality, preserved in alcohol.

Type locality: "Mussel Valley" site, North Fiji Basin, 18°50'S, 173°29'W, 2765 m, STARMER II, dive PL 18, Y. Nojiri, observer. 13 July 1989.

Description: Shell large, up to 155 mm long, very thin and on ventral margin somewhat "elastic," quite fragile, elongate-modioliform, variable in outline and tumidity but generally very inflated, equivalve, length/height ratio 1.9–2.5. Juvenile specimens shorter and less tumid than adults. Beaks well subterminal, at one-fifth to one-sixth of total shell length. Anterior margin generally rather narrowly rounded, ventral margin straight, slightly convex, or, in fully grown specimens, occasionally somewhat concave in middle part. Posterior margin ventrally more or less broadly rounded, postero-dorsal margin behind ligament slightly to markedly convex; postero-dorsal corner narrowly rounded to indistinct. Ligament plate slightly arched to nearly straight. Exterior with well-developed, irregular growth lines and with tendency to somewhat irregular, narrow to rather broad concentric grooves and striae, mostly on ventral part of valves, often extending forward to anterior part, occasionally smaller and quite regular in middle part (Figure 19). In fully grown specimens, faint, broad radial undulations frequently visible on postero-dorsal slope, bifurcating and somewhat reminiscent of the sculpture of *Brachidontes* (Figures 12, 16). Several specimens with 4–6 broad and very faint transverse waves in middle of shell which occasionally cause undulation of concentric striae and may be marked by darker color of periostracum (Figures 15, 18). Umbo broad and somewhat flattened.

Shell without periostracum dull whitish; interior nacreous.

Periostracum strong, light chestnut brown, posterior umbonal region lighter brown, smooth, glossy, with no periostracal hairs but with byssal endplates of other specimens scattered over valve. Small, juvenile specimens with periostracum yellow.

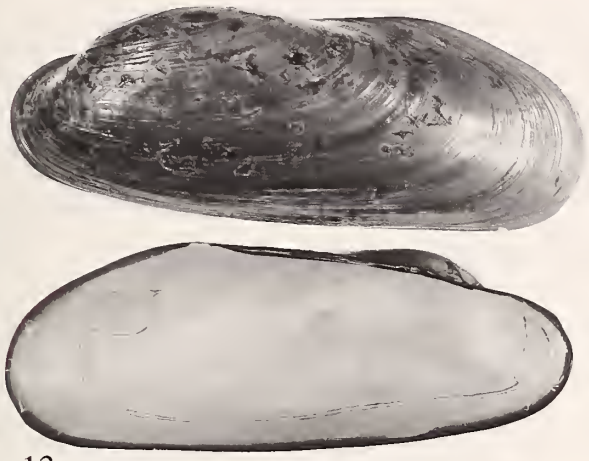
Hinge without teeth, anterior hinge margin hardly protruding toward ventral. Ligament opisthodetic, moderately strong, extending to just in front of postero-dorsal corner. Subligamental shell ridge very faint from under umbos to middle of ligament, then becoming obsolete, under beaks visible only in ventral and not in lateral view (Figure 20). Anterior adductor scar broadly crescent-shaped, well in front of umbo. Posterior adductor scar rounded-trapezoid, united with posterior scar of posterior pedal and byssus retractor muscle. Anterior scar of same muscle separated, rather small and situated under ligament, at about two-thirds of it, in juvenile specimens (up to about 40–45 mm) located under end of ligament. Anterior byssus retractor scar in anterior part of umbonal cavity, just in front of beaks, visible only in posterior and ventral view but not in lateral view of interior. Pallial line only very weakly concave to straight.

Animal with very large ctenidia which are slightly more than three-fourths of shell length; outer and inner demibranch of nearly equal size (Figure 14). Mantle lobes separate from anterior end to postero-ventral extremity of shell margin. Mantle folds on anterior end passing ventrally over anterior adductor muscle fore- and upward along anterior margin for rather long distance, then folding

→

Explanation of Figures 13–20

Figures 13–18. *Bathymodiolus **elongatus*** von Cosel, Métivier & Hashimoto, sp. nov. "Mussel Valley" site, STARMER II, dive PL 18. Figure 13. Paratype, LACM 2760, 125.8 mm. Exterior and interior of left valve. Strongly elongate specimen. Figure 14. Paratype, MNHN, 112.0 mm., Exterior of right valve and general view of preserved animal, right valve and mantle removed. Notice the large gills, the small foot and the small right labial palp just in front of the foot. Figure 15. Paratype, AMS C200706, 103.6 mm. Half-ventral view to show the undulations of the concentric striae in the middle near the ventral margin. Figure 16. Paratype, SMF 310427, 122.6 mm. Exterior of right valve. Note the shallow bifurcating radial undulations on the posterior part. Figure 17. Same specimen as on Figure 13. Interior and exterior of right valve. Figure 18. Paratype, MNHN, 95.1 mm. Exterior of left valve, showing black-marked transverse waves on the ventral part. Figure 19. *Bathymodiolus **elongatus*** von Cosel, Métivier & Hashimoto, sp. nov., STARMER II, dive PL 19, 96.3 mm. Exterior of left valve of a specimen showing quite regular concentric striae. Figure 20. *Bathymodiolus **elongatus*** von Cosel, Métivier & Hashimoto, sp. nov. Paratype, MNHN, STARMER II, dive PL 18, 131.5 mm. Interior of left valve and ventral view to show position of foot/byssus retractor muscle scars.



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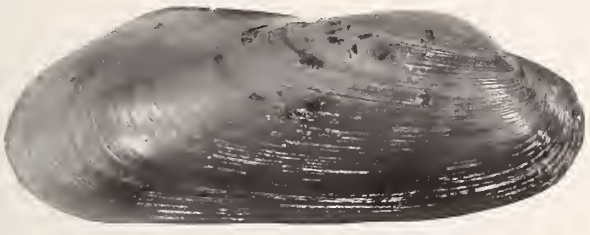

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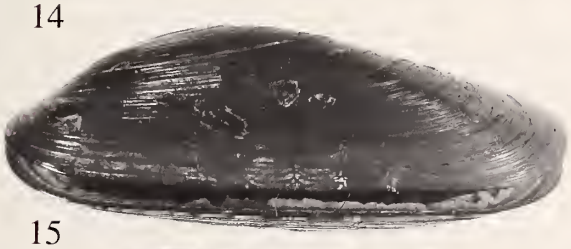

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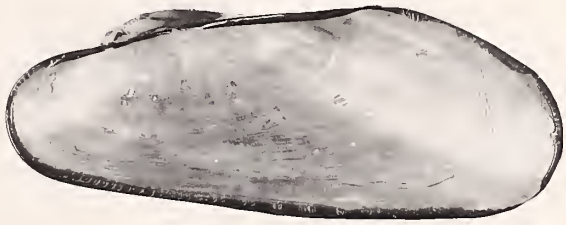

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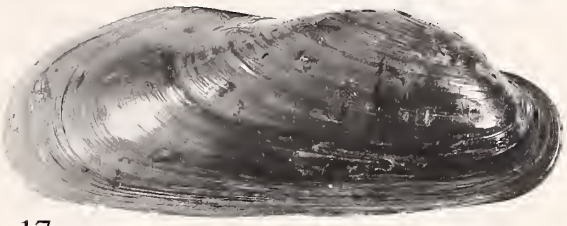

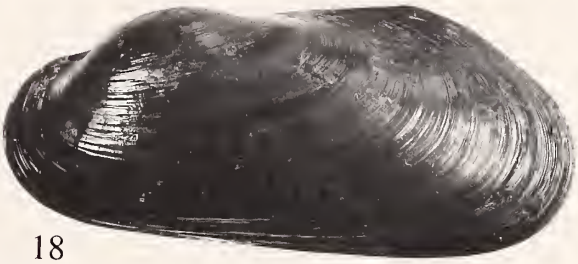

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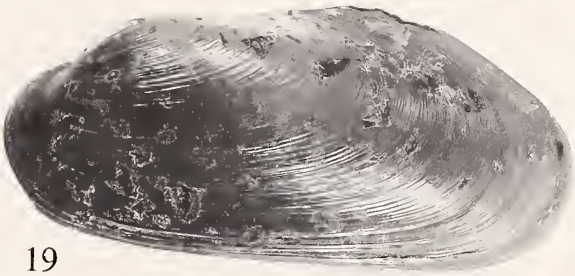

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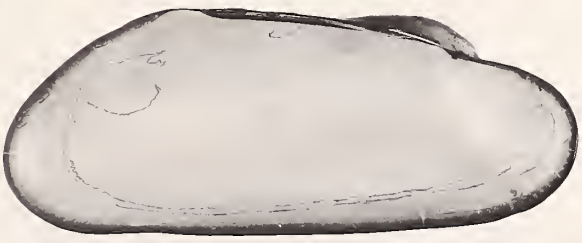

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down- and backward to again pass lower end of anterior adductor muscle toward ventral margin (Figure 25, left). Valvular siphonal membrane short and rather thin, reaching from postero-ventral corner to siphonal opening; no papilla present toward anterior margin (Figure 25, right). Foot thick, very broad and flattened, foot-byssus retractor muscle complex with rather short anterior retractor. Posterior byssus retractors consisting of two diverging muscle bundles with common base at base of byssus. Anterior bundle more or less short and broad and arising rather steeply toward attachment point on shell interior; posterior bundle long and thinner, passing at very low angle to longitudinal shell axis toward attachment point directly above and in front of posterior adductor. Posterior foot retractor well developed, arising from extreme anterior side of foot base, well in front of base of byssus retractor muscles, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor, reaching shell inside closely appressed to it over about half its length or more. Labial palps narrow-triangular, small but thick, anterior two slightly smaller than posterior pair.

Selected measurements (length, height, tumidity) with length-height ratios (all STARMER, sta. PL 18):

156.2 × 64.5 × 63.2 mm paratype MNHN	2.4
140.6 × 56.6 × 57.0 mm holotype	2.5
134.9 × 55.6 × 51.7 mm paratype MNHN	2.4
132.4 × 56.3 × 48.6 mm paratype MNHN	2.4
130.8 × 51.3 × 51.9 mm paratype MNHN	2.6
125.7 × 46.0 × 51.0 mm paratype LACM	2.7
122.6 × 47.0 × 46.7 mm paratype SMF	2.6
121.1 × 47.1 × 53.0 mm paratype NSMT	2.6
119.4 × 49.4 × 51.1 mm paratype USNM	2.4
113.6 × 42.0 × 46.0 mm paratype SMF	2.7
111.7 × 45.4 × 46.7 mm paratype LACM	2.5
111.2 × 43.6 × 44.8 mm paratype USNM	2.6
111.1 × 43.7 × 45.4 mm paratype MCZ	2.5
106.7 × 46.1 × 41.8 mm paratype AMS	2.3
105.6 × 41.5 × 43.8 mm paratype BMNH	2.5
103.8 × 42.6 × 42.2 mm paratype ZMB	2.4
103.5 × 44.6 × 37.0 mm paratype AMS	2.3
100.8 × 45.5 × 39.0 mm paratype NMNZ	2.2
99.8 × 41.8 × 37.8 mm paratype ZMB	2.4
95.5 × 38.8 × 35.7 mm paratype NSMT	2.4
95.1 × 37.7 × 35.3 mm paratype MCZ	2.5
94.5 × 39.1 × 38.5 mm paratype MCZ	2.4
90.6 × 40.4 × 36.2 mm paratype BMNH	2.3
85.5 × 37.2 × 33.2 mm paratype MNHN	2.3
69.5 × 32.5 × 26.9 mm paratype MNHN	2.1
57.7 × 28.8 × 21.3 mm paratype MNHN	2.0
52.2 × 26.6 × 18.3 mm paratype MNHN	2.0
41.2 × 23.1 × 15.1 mm paratype MNHN	1.8

Material examined: Type material; other material: North Fiji Basin, "Mussel Valley" site, 18°50′S, 173°29′W, 2765 m, STARMER II, dive PL 18, Y. Nojiri, observer. 13 July 1989, 106 spm.; STARMER II, dive 19, same locality and coordinates, 29 spm., all MNHN.

Habitat: The specimens were found byssally attached to lava around diffuse vents. The habitat is characterized by the absence of massive hydrothermal deposits and by low temperature vent fluids not exceeding 8.5°C. The fluid venting was confirmed with the naked eye as "shimmering." Slender vestimentiferans, limpets (*Lepetodrilus elevatus*), bythograeid crabs (*Austinograea* cf. *williamsi*), and galatheids were found in the diffuse vent areas. For description of the site, see Jollivet et al. (1989).

Distribution: Known only from the North Fiji Basin.

Etymology: "Slender" (Latin: *elongatus*) was the working name for this mussel.

Remarks: No substantial differences were observed in the soft parts between *B. **elongatus*** and *B. **brevior***. The valvular siphonal membrane seems thinner and slightly broader in the preserved specimens of *B. **elongatus***, and the "back-folding" of the mantle lobes around the anterior adductor is more conspicuous (see Figure 25 vs. Figure 26). The configuration of the foot-byssus retractor complex is similar in both species; however, in *B. **elongatus***, the anterior retractor is slightly shorter, and the posterior bundle of the posterior byssus retractor somewhat longer.

The shell of *B. **elongatus*** is easily distinguished from that of *B. **brevior*** by its markedly more slender, more elongate, and more tumid shape; the anterior end is narrower, and the beaks are situated still more backward. The length-height ratios of both species are plotted against shell length in Figure 37; they are substantially different in both species, and their change with size indicates allometric growth, which, however, is much more pronounced in *B. **elongatus***.

For *B. **brevior***, the graph shows a higher variability within the species, paired with a much less significant correlation between size and length-height ratio. The mean ratios are 1.95 for *B. **brevior*** and 2.30 for *B. **elongatus*** (see Table 3). The allometric growth of both species also causes the change of position with growth of the anterior portion of the posterior byssus-retractor scar from below the end of the ligament forward to below two-thirds of it.

The postero-dorsal margin behind the almost straight ligament plate is variable, from slightly to markedly convex, and, as a consequence, the postero-dorsal corner is narrowly rounded as in *B. **brevior***, or indistinct. Moreover, *B. **elongatus*** has a much thinner and more fragile shell than *B. **brevior***; the "elasticity" of the valves is demonstrated by the fact that on abrupt tight closing by the adductors, the ventral margin of one valve gives way to that of the other valve, and thus the ventral margins of the two valves appear slightly discordant. The anterior byssus retractor muscle scar is situated slightly more forward. The periostracum of *B. **elongatus*** is thinner and lighter colored than in most *B. **brevior***. As in *B. **brevior***, the ligament ends abruptly, but is somewhat shorter in relation to the total shell length.

Bathymodiolus thermophilus is less slender and more compressed with less prominent beaks; the beaks are situated more forward, the ligament is still shorter in relation to total shell length than in *B. **elongatus***, and the scar of

Table 1

Comparison of some features in *Bathymodiolus*.

	B. thermophilus (from 13°N)	*B. brevior*	*B. elongatus*	*B. puteoserpentis*
General shell form	moderately elongate	somewhat stout	elongate	somewhat stout
Tumidity	more or less compressed	tumid	very tumid	moderately tumid
Shell	thin but solid	thin but solid	very thin and more fragile	thin but solid
Position of anterior part of posterior byssus retractor muscle scar	under the end of the ligament	at ⅔ of the ligament	at ⅔ of the ligament	under posterior third of ligament, near the end
Position of anterior byssus retractor scar in the umbonal cavity	slightly behind the beak	under and in front of the beak	under and in front of the beak	under and in front of the beak
Ventral pallial line	markedly deflected	nearly straight	straight	nearly straight
Mantle lobes on anterior half of ventral side	fused	separate	separate	separate
Valvular siphonal membrane	long and thin	short, narrow, rather strong	short	short
Posterior end of ligament	tapering	abrupt	abrupt	abrupt to slightly tapering
Subligamental shell ridge	strong and angular	faint from umbo to ligament middle, then obsolete	very faint from umbo to ligament middle, then obsolete	faint to obsolete, occasionally more marked

Table 2

Bathymodiolus ***brevior***, length/height ratios from different localities.

	Ratio	Mean	SD	SE	*n*	Length (mm)	Mean
Regions							
N-Fiji Basin	1.7–2.2	1.945	0.115	0.018	39	40.4–137.2	92.6
Lau Basin	1.6–2.2	1.951	0.103	0.007	214	33.2–143.5	83.8
Hydrothermal fields							
Vailili	1.7–2.2	1.955	0.148	0.028	29	33.2–143.5	94.2
Hine Hina	1.6–2.2	1.950	0.094	0.007	185	45.5–111.1	82.1
White Lady	1.7–2.2	1.940	0.117	0.019	38	40.4–137.2	92.1
Mussel Valley	2.0	2.0	—	—	1	111.7	
Stations (dives)							
Hine Hina BL 01	1.6–2.2	1.945	0.110	0.014	63	45.5–104.2	84.2
Hine Hina BL 03	1.7–2.2	1.942	0.083	0.008	106	48.1–104.6	79.9
Hine Hina BL 05	1.9–2.2	2.020	0.069	0.017	16	65.7–111.1	88.6
Vailili BL 04	1.7–1.9	1.832	0.082	0.024	12	33.2–81.1	69.9
Vailili BL 12	1.8–2.2	2.042	0.120	0.029	17	49.6–143.5	111.4
White Lady PL 10	1.9–2.1	1.926	0.079	0.036	5	100.0–112.5	107.7
White Lady PL 11	1.9–2.2	2.008	0.113	0.051	5	90.0–137.2	110.5
White Lady PL 13	1.7–1.9	1.821	0.059	0.030	4	64.2–110.0	81.1
White Lady PL 20	1.7–2.2	1.955	0.120	0.025	24	40.4–129.3	86.8
Mussel Valley PL 19	2.0	—	—	—	1	111.7	
B. brevior "Sonne"	1.5–2.2	1.837	0.161	0.032	25	17.2–123.3	63.3

Table 3

Comparisons of length/height ratios of *Bathymodiolus* ***brevior*** and *Bathymodiolus* ***elongatus***.

	Length/height ratio				
	Ratio	Mean	SD	SE	*n*
B. ***brevior*** total	1.6–2.2	1.950	0.105	0.007	253
B. ***elongatus*** total	1.8–2.8	2.297	0.179	0.015	149
B. ***brevior*** 90 mm and larger	1.8–2.2	2.010	0.084	0.009	90
B. ***elongatus*** 90 mm and larger	2.2–2.8	2.397	0.115	0.012	93
B. ***brevior*** smaller than 90 mm	1.6–2.2	1.914	0.099	0.008	158
B. ***elongatus*** smaller than 90 mm	1.8–2.4	2.123	0.136	0.019	53
B. ***brevior*** 60 mm and smaller	1.6–2.0	1.830	0.147	0.042	12
B. ***elongatus*** 60 mm and smaller	1.8–2.2	1.994	0.114	0.028	17
B. ***brevior*** 50 mm and smaller	1.6–2.0	1.757	0.143	0.054	7
B. ***elongatus*** 50 mm and smaller	1.8–2.0	1.880	0.007	0.029	6

Comparison (* = significative at 95%)			
	Mean diff.	Fisher PLSD	Scheffe F-test
B. ***elongatus*** vs. *B.* ***brevior*** total	0.347	0.028*	602.297*
B. ***elongatus*** vs. *B.* ***brevior*** 90 mm and larger	0.386	0.029*	673.987*
B. ***elongatus*** vs. *B.* ***brevior*** smaller than 90 mm	0.209	0.034*	144.212*
B. ***elongatus*** vs. *B.* ***brevior*** 60 mm and smaller	0.163	0.099*	11.341*
B. ***elongatus*** vs. *B.* ***brevior*** 50 mm and smaller	0.123	0.142	3.611

the anterior part of the posterior byssus retractor is situated under the posterior end of the ligament. As in most *B.* ***brevior*** specimens, the periostracum of *B.* ***elongatus*** tends more toward a chestnut color than to the olive coloration observed in many specimens of *B. thermophilus*.

Although the differences in length/height ratio and coloration between *B.* ***elongatus*** and *B.* ***brevior*** are rather constant, there are specimens of *B.* ***brevior*** which seem to have a slightly tendency toward intergradation to *B.* ***elongatus***, especially specimens from dive BL 05 at Hine Hina (BIOLAU cruise). These have a clear brown periostracum like *B.* ***elongatus*** and a slightly higher mean length/height ratio (2.02) than the "average" *B.* ***brevior*** (1.95, see Table 2) which, however, is still much lower than that of *B.* ***elongatus*** (2.18).

A one-way analysis of variance (ANOVA) including all available specimens was run to test the significance of the differences between *B.* ***brevior*** and *B.* ***elongatus*** in length/height ratio ($F = 602.297$; $df = 1, 400$, $P < 0.001$) and length/tumidity ratio ($F = 50.533$; $df = 1, 398$, $P < 0.001$). In both parameters, the difference is significant at 95%.

1/h ratio:	mean difference:	0.347
	Fisher PLSD:	0.028*
	Scheffe F-test:	602.297*
1/tumidity ratio:	mean difference:	0.125
	Fisher PLSD:	0.035*
	Scheffe F-test:	50.533*

Separate calculations for the length-height ratio of *B.* ***brevior*** from the different localities showed only very slight and mostly non-significant differences.

* Significant at 95%.

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Explanation of Figures 21–24

Figures 21–22. *Bathymodiolus* ***puteoserpentis*** von Cosel, Métivier & Hashimoto, sp. nov. "L'Elan" site, Snake Pit hydrothermal field, Mid-Atlantic Ridge, 23°22'N, 47°57'W, 3515 m, HYDROSNAKE, dive HS 03. Figure 21. Holotype, MNHN, 112.3 mm. Exterior and interior of left valve, ventral view of left valve to show position of foot/byssus retractor muscle scars, dorsal view to show tumidity. Figure 22. Paratype, MNHN, 94.5 mm. Interior and exterior of left valve. Figures 23–24. *Bathymodiolus thermophilus* Kenk & Wilson. East Pacific Rise (13°N). Figure 23. 152.0 mm, BIOCYARISE '84, PL 45. Exterior and interior of left valve. Figure 24. 104.7 mm, HERO '92, dive 2523, Site "Genesis." Interior and exterior of left valve, ventral view of left valve to show position of foot/byssus retractor muscle scars (note the prominent subligamental shell ridge); dorsal view.

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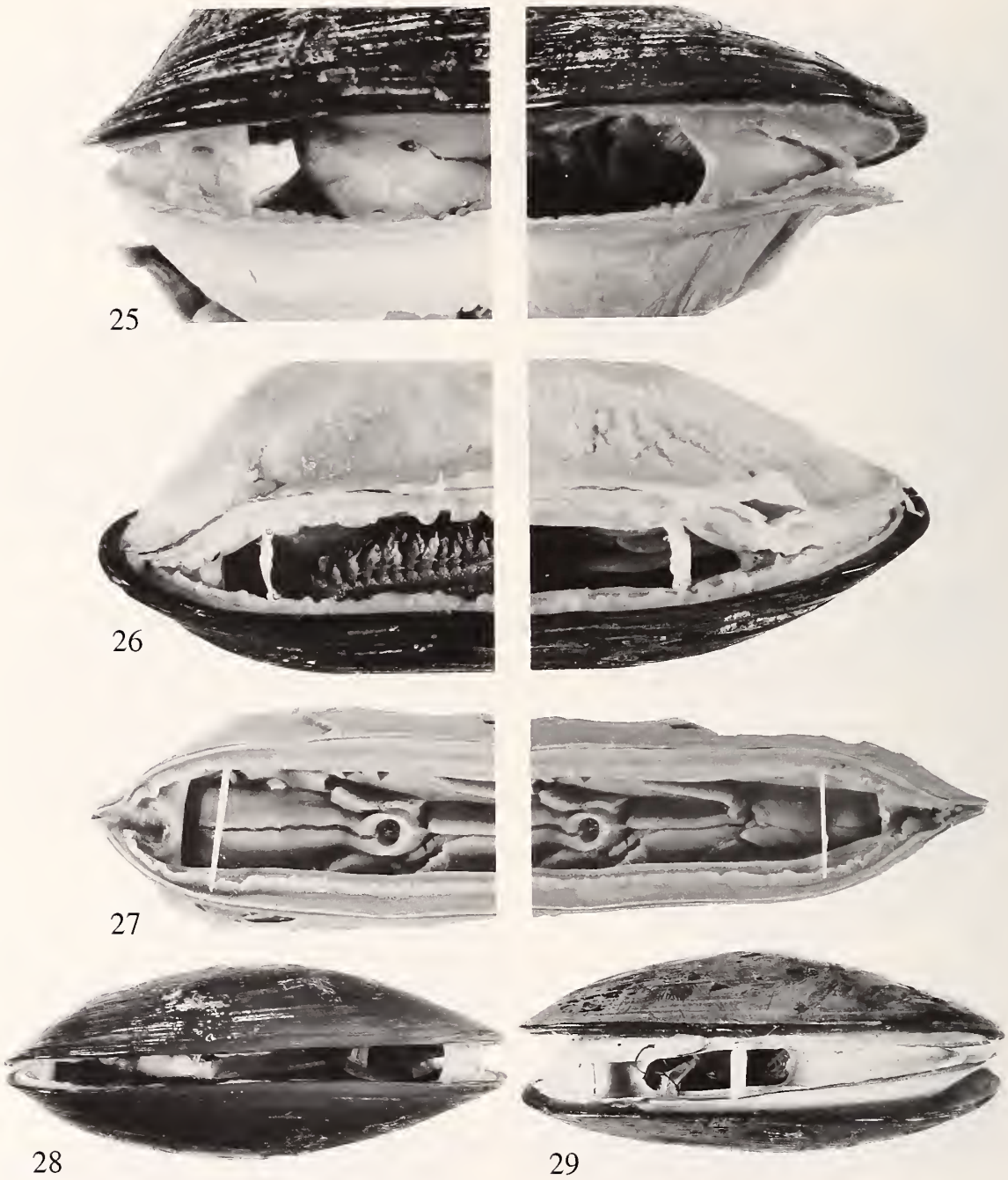
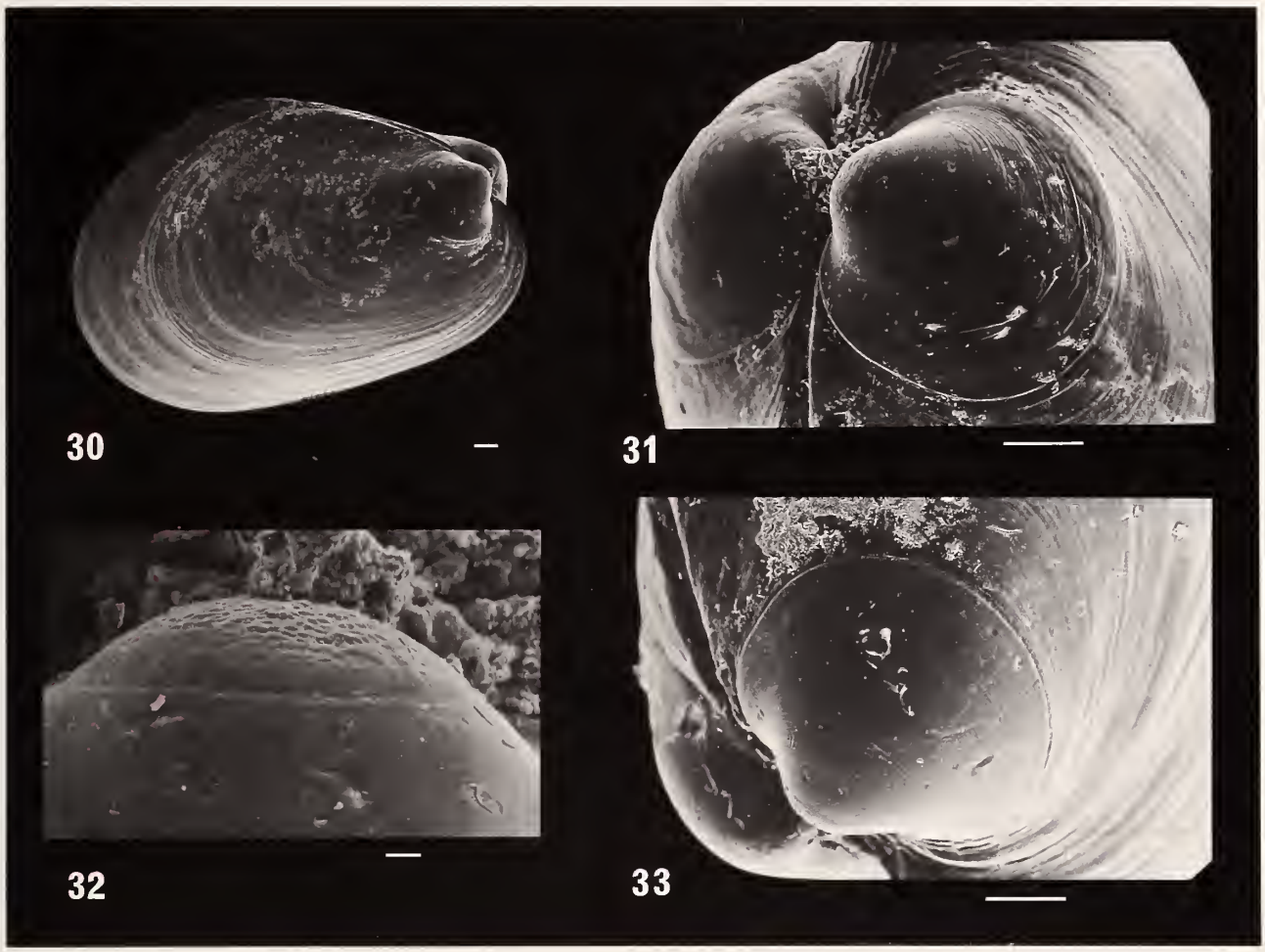


Explanation of Figures 25–29

Figure 25. *Bathymodiolus* ***elongatus*** von Cosel, Métivier & Hashimoto, sp. nov. Holotype. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane. The anterior fusion is "turning back" above the anterior adductor. The posterior fusion is at the posterior end, posterior to the valvular membrane. Figure 26. *Bathymodiolus* ***brevior***, von Cosel, Métivier & Hashimoto, sp. nov. Specimen from "Mussel Valley." Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane (the sticks keep the mantle openings open). Figure 27. *Bathymodiolus* ***puteoserpentis*** von Cosel, Métivier & Hashimoto, sp. nov. Close-up view of anterior and posterior mantle fusion and posterior valvular siphonal membrane (the sticks keep the mantle openings open). Figure 28. *Bathymodiolus* ***elongatus*** von Cosel, Métivier & Hashimoto, sp. nov. Paratype, SMF 310427 (see also Figure 16). Ventral view. Figure 29. *Bathymodiolus thermophilus* Kenk & Wilson. East Pacific Rise (13°N), HERO '92, Sta. 2523. Same specimen as on Figure 24. Ventral view. Comparison of both species to show extension of ventral opening.



Explanation of Figures 30–33

Figures 30–33. *Bathymodiolus* ***brevior*** von Cosel, Métivier & Hashimoto, sp. nov. BIOLAU, dive BL 03. SEM micrographs of embryonic and postembryonic shells. Figure 30. Juvenile specimen. Scale bar: 100 μm. Figure 31. Protoconch I and II of the same specimen. Scale bar: 100 μm. Figure 32. Close-up view of protoconch I. Scale bar: 10 μm. Figure 33. Protoconch II of another specimen of the same lot. Scale bar: 100 μm.

Bathymodiolus ***puteoserpentis*** von Cosel, Métivier & Hashimoto sp. nov.

(Figures 21–22, 27, 36, 38)

Bathymodiolus n. sp., Tunnicliffe, 1991:349

Type material: Holotype, MNHN, HYDROSNAKE expedition, Snake Pit hydrothermal field, Mid-Atlantic Ridge; 2 paratypes with preserved animal, same locality, in MNHN, 1 in MCZ; 5 paratypes, same locality, empty shells but live-collected: 1 in MNHN, 1 in NSMT, 1 in USNM, 1 in LACM, 1 in SMF.

Type locality: "L'Elan" (The Moose) site, Snake Pit hydrothermal field, Mid-Atlantic Ridge, 23°22′N, 47°57′W, 3515 m, HYDROSNAKE dive HS 03, J. Karson, observer, 21 June 1988.

Description: Shell rather large, up to 119 mm long, quite thin but solid, oval-modioliform, variable in outline and tumidity, equivalve, length/height ratio 1.8–2.0. Juvenile specimens more oval and more compressed than adults. Beaks subterminal, at one-seventh of total shell length. Anterior margin broadly to rather narrowly rounded, ventral margin straight or very weakly convex, in middle section or just before middle often somewhat concave. Postero-ventral margin broadly rounded, continuing to markedly convex postero-dorsal margin and more or less broadly rounded postero-dorsal corner. Ligament plate slightly arched in anterior part, tending toward straight in pos-

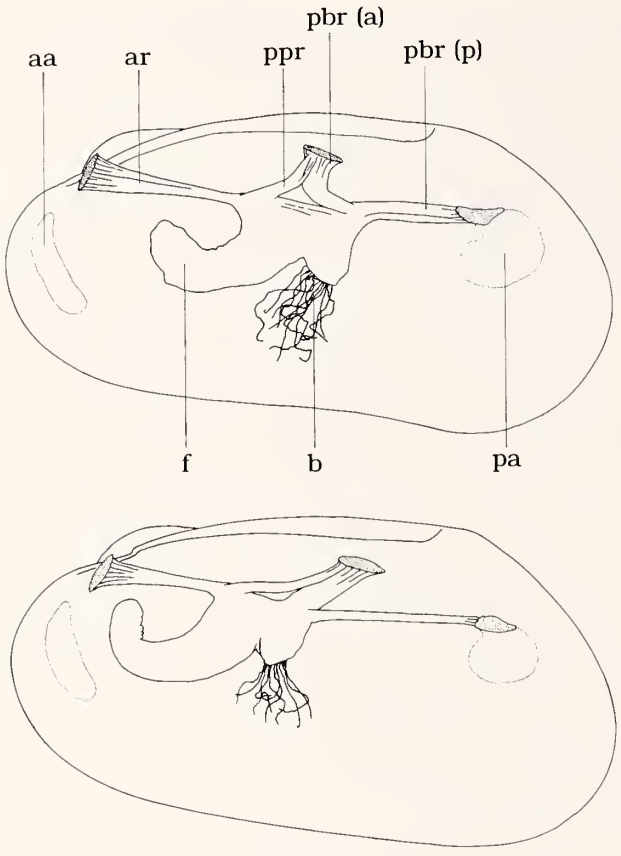


Figure 34

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus* ***brevior*** von Cosel, Métivier & Hashimoto, sp. nov. and its position in the shell (separate slender strand of anterior retractor muscle serving as support for labial palps not drawn; ligament's position only marked). Above, specimen from BIOLAU BL 12, 89.1 mm, paratype MNHN; below, specimen from BIOLAU sta. BL 1, 90.2 mm (the different lengths of the corresponding muscle bundles in both specimens seem to be due to different degree of contraction in the moment of preservation). aa, position of anterior adductor; ar, anterior retractor muscle; ppr, posterior pedal retractor; pbr (a), posterior byssus retractor, anterior bundle; pbr (p), posterior byssus retractor, posterior bundle; f, foot; b, byssus; pa, position of posterior adductor.

terior part. Exterior smooth, with pronounced irregular growth lines. Umbo broad, somewhat flattened.

Periostracum strong, dark brown, and rather glossy. Valves irregularly covered with byssal endplates of other specimens, which in dried shells peel off.

Interior of valves white and nacreous.

Hinge without teeth but anterior hinge margin slightly protruding toward ventral. Ligament opisthodetic, strong, extending over most of postero-dorsal margin, leaving free very short part just in front of postero-dorsal corner. Subligamental shell ridge usually faint to obsolete; in some specimens, however, quite well marked. Anterior adductor scar rather broad and nearly half-moon-shaped, situated in front of umbo. Posterior adductor scar large, united with posterior scar of posterior pedal and byssus retractor muscle; anterior scar of muscle separated and situated under posterior third of ligament or nearly under ligament's end. Anterior byssus retractor muscle scar in anterior part of umbonal cavity, just under beak, in extreme lower part occasionally visible in lateral view of interior of valve. Pallial line rather close to margin and nearly parallel to it.

Animal with very large ctenidia which are more than three-fourths of shell length; outer and inner demibranch of nearly equal size. Mantle lobes separate from anterior end to posterior shell margin, valvular siphonal membrane beginning at postero-ventral extremity of shell margin (a photo cannot be shown because in all available specimens, the adductors had been cut on board before preservation to allow quick entry of the preservation liquid via the open valves). Foot not very thick, flattened, tapering toward end and terminating in rather narrow tip, with ventral byssal groove three-fourths of foot length. Foot-byssus retractor muscle complex with moderately long anterior retractor. Posterior byssus retractors consisting of two strong, diverging muscle bundles with common base at base of byssus. Anterior bundle broad and arising steeply toward attachment point on shell inside. Posterior bundle long, rather strong, divided into two parallel bundles at about half its length (in observed specimen), passing at low angle to longitudinal shell axis toward attachment point directly in front and above posterior adductor. Posterior foot retractor broad, arising from base of foot, well in front of base of byssus retractor muscles, passing outer side of anterior retractor toward anterior bundle of posterior byssus retractor and reaching shell inside closely appressed to it, touching it at half to two-thirds its length. Labial palps triangular, small but thick, anterior two slightly smaller than posterior pair.

Measurements (length, height, tumidity) with length-height ratios:

112.2 × 56.3 × 51.2 holotype	HS 03	2.0
94.4 × 46.2 × 45.5 paratype MNHN	HS 03	2.0
85.2 × 48.4 × 39.0 paratype SMF	HS 03	1.8
82.6 × 45.0 × 37.3 paratype MNHN	HS 03	1.8
81.1 × 40.0 × 31.5	HS 10	2.0
80.4 × 45.6 × 38.1 paratype NSMT	HS 03	1.8
80.2 × 39.4 × 31.4	HS 10	2.0
76.1 × 40.2 × 32.5	HS 10	1.9
71.7 × 36.1 × 27.3	HS 10	2.0
71.3 × 38.5 × 34.2 paratype LACM	HS 03	1.9
68.0 × 34.5 × 28.3	HS 10	2.0
65.6 × 34.2 × 27.0	HS 10	1.9
60.4 × 37.2 × 31.2 paratype MCZ	HS 03	1.6
57.0 × 31.7 × 25.4 paratype USNM	HS 03	1.8

Material examined: Type material; other material: "Les Ruches" site, Snake Pit area, Mid-Atlantic Ridge, HYDROSNAKE expedition, dive HS 10, same coordinates, 3478 m, M. Segonzac, observer, 29 June 1988, 6 spm.,

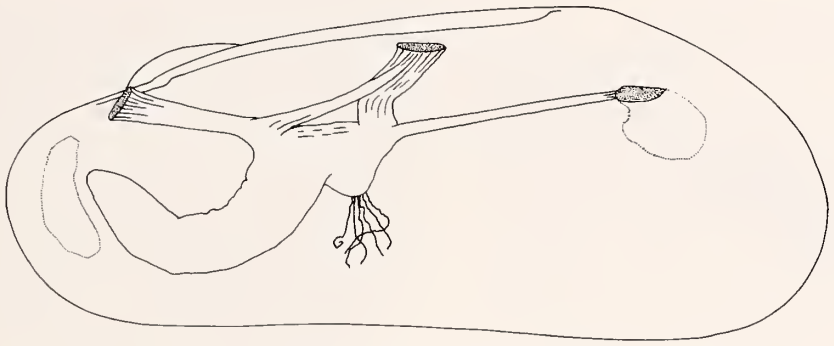


Figure 35

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus* ***elongatus*** von Cosel, Métivier & Hashimoto, sp. nov. and its position in the shell. Specimen from STARMER sta. PL 19, 98.7 mm. For explanations, see previous figure.

MNHN (of a total of 23 specimens collected, 14 were available for this study).

Habitat: Byssally attached to sulphur blocks immediately around diffuse venting of water (Desbruyères, 1989; Segonzac, 1992).

Distribution: Known only from the Snake Pit area, Mid-Atlantic Ridge. The site is described by Mevel et al. (1989).

Etymology: The species is named after the site: *puteus* (Latin) = pit; *serpens* (Latin) = snake.

Remarks: The foot-byssus retractor complex of *B.* ***puteoserpentis*** (Figure 36) more closely resembles that of *B. thermophilus* (as figured in Kenk & Wilson (1985)) than those of *B.* ***brevior*** and *B.* ***elongatus***; the anterior bundle of the posterior byssus retractor is longer; the posterior bundle is stronger. The other observed anatomical characters are as in *B.* ***brevior*** and *B.* ***elongatus***.

The shell of *B.* ***puteoserpentis*** in some aspects resembles that of *B. thermophilus,* but it is shorter and somewhat broader, a bit more inflated with a longer ligament in relation to shell length, a more forward-situated anterior byssus/foot retractor muscle scar, and chestnut-brown rather than olive-brown periostracum (as in the few examined *B. thermophilus*). *Bathymodiolus thermophilus* and *B.* ***puteoserpentis*** both have the anterior part of the byssus retractor scar located nearly below the end of the ligament and not at two-thirds the length of the ligament as in *B.* ***brevior*** and *B.* ***elongatus***. There seems to be only a slight change of position with growth, judging from the smallest specimen seen (57 mm). The shell outline of *B.* ***puteoserpentis*** is roughly similar to that of *B.* ***brevior,*** but the Atlantic species seems to be more variable. The length/

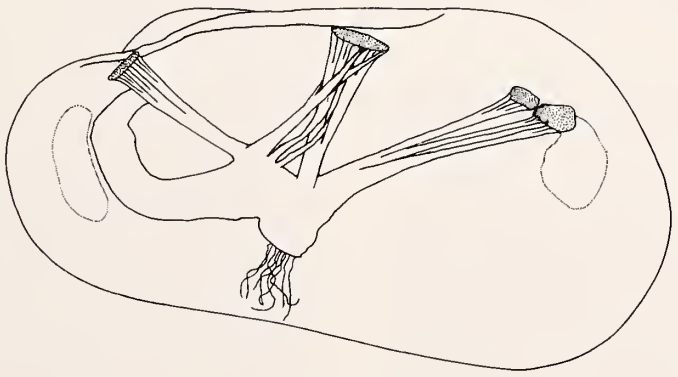


Figure 36

Sketch of foot-byssus retractor muscle complex of *Bathymodiolus* ***puteoserpentis*** von Cosel, Métivier & Hashimoto, sp. nov. and its position in the shell. Specimen from HYDROSNAKE sta. HS 03, 82.6 mm, paratype MNHN. For explanations, see Figure 34.

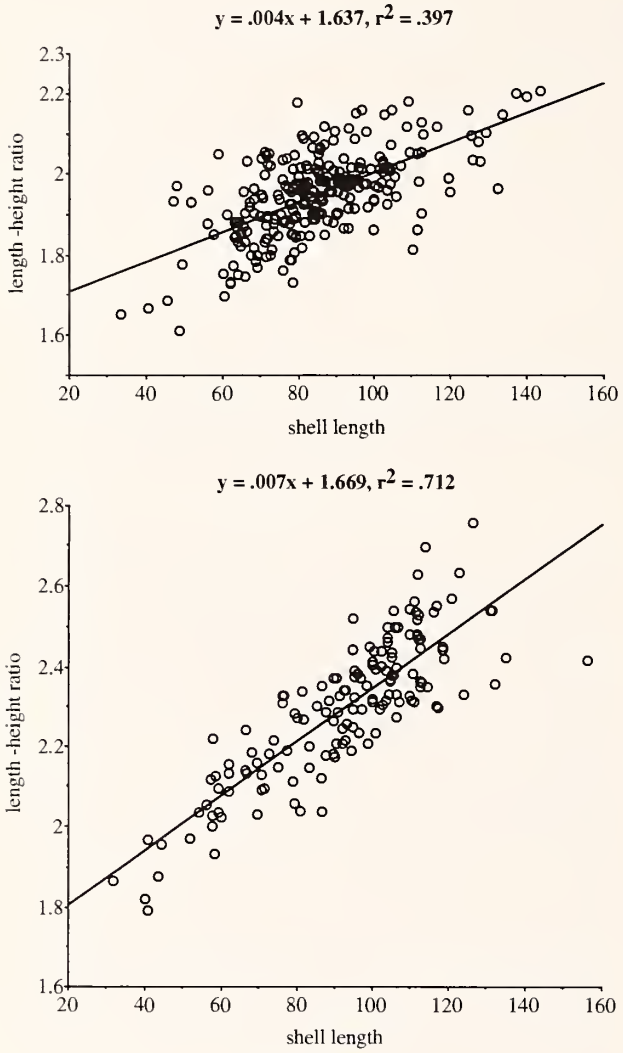


Figure 37

Length-height ratio vs. shell length in mm of *Bathymodiolus* ***brevior*** von Cosel, Métivier & Hashimoto, sp. nov. (all stations, n = 253) and *B. elongatus* (all stations, n = 49).

height ratio coincides with that of *B.* ***brevior,*** but is significantly different from that of *B.* ***elongatus*** (Figure 38).

DISCUSSION

The separation of *B.* ***brevior,*** *B.* ***elongatus,*** and *B.* ***puteoserpentis*** is based mainly on shell characters. The differences in shell shape between *B.* ***brevior*** and *B.* ***elongatus*** are quite evident in half-grown and adult specimens, but less evident in juvenile specimens. In very young specimens (under 50 mm), the differences are no longer significant (Table 3). In spite of the very close relationship, the differences in shell shape and thickness, as well as the sympatric occurrence of *B.* ***brevior*** and *B.* ***elongatus*** on one diving station (Mussel Valley, PL 19), leads us to

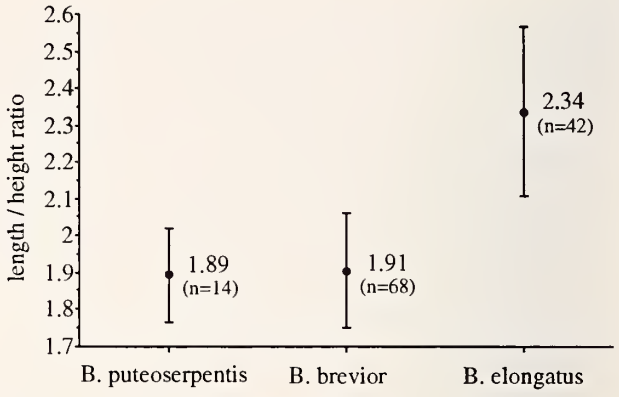


Figure 38

Length-height ratios of *Bathymodiolus* ***elongatus,*** von Cosel, Métivier & Hashimoto, sp. nov. *B.* ***brevior*** von Cosel, Métivier & Hashimoto, sp. nov. and *B.* ***puteoserpentis*** von Cosel, Métivier & Hashimoto, sp. nov. (Bars are 1 SD).

identify two different species although there seems to be a very slight tendency to intergrade.

The larval shell of *B.* ***brevior*** has a small protoconch I (100 μm in length) and a large protoconch II (400 μm in length), similar to *B. thermophilus* (Lutz et al., 1980).

The main differences between the three species here described and *B. thermophilus* are the fusion of the inner mantle folds along the anterior half of the ventral margin as well as a long valvular siphonal membrane in *B. thermophilus* (Figure 29) and the absence of this fusion and a short valvular siphonal membrane in the three new species (Figures 25–28). The foot-byssus retractor muscle complex exhibits the same basic configuration in all four species; however, in *B. thermophilus,* the anterior retractor attaches in the posterior part of the umbonal cavity, whereas in the three new species, it attaches on its anterior wall. The other differences between the retractor complexes are less conspicuous and concern the relative length and thickness of the different muscle bundles: in *B.* ***brevior*** and *B.* ***elongatus,*** the anterior bundle of the posterior byssus retractor tends to be shorter; it attaches more anteriorly in adult specimens; the posterior bundle tends to be thinner; the bundles are also more widely divergent than in *B.* ***puteoserpentis*** and *B. thermophilus.*

The assignment of the new species to *Bathymodiolus* is provisional. Of the possible genera *Adipicola* Dautzenberg, 1927 *Idasola* Iredale, 1915 (= *Idas* Jeffreys, 1876, *non* Mulsant, 1876; see Dell, 1987), *Benthomodiolus* Dell, 1987, and *Bathymodiolus,* the latter seems at the moment to be the most appropriate genus. *Adipicola* has an entirely different byssus retractor muscle system with no separate foot retractor (see Dell, 1987:fig. 42). In *Idasola,* the hinge line has typical, close-set vertical grooves, and the shell has periostracal bristles. Both characters are absent in our hydrothermal vent mussels; also the foot-byssus retractor muscle complex is different, and the posterior pedal re-

tractor and posterior byssal retractor are together in one (or two) bundles (see Dell, 1987:fig. 38–43). Apart from the size, the shells of *Benthomodiolus* are rather similar in shape to the new species, and also the foot-byssus retractor complex has the same general arrangement, although the posterior foot retractor is thinner in the two known *Benthomodiolus* (Dell, 1987, figs. 51, 52) than in our species. However, the presence of periostracal hairs in *Benthomodiolus* and their absence in *Bathymodiolus thermophilus,* as well as in the new species, is a reason for rejecting *Benthomodiolus* and placing our species for the moment in *Bathymodiolus*.

The presence or absence of the inner mantle fold fusion and differences in the valvular siphonal membrane are evidence for ultimately separating the new species from *Bathymodiolus* and establishing a new genus; however, a new genus should be erected only after a more thorough study of the internal anatomy of the new species (study currently under way by M. Le Pennec and A. Fiala) as well as study of the other deep-water mytilid genera.

The above mentioned differences between the eastern Pacific and western Pacific populations of hydrothermal vent mussels, as well as the differences in shell shape and positions of the adductor and foot-byssus retractor muscles, lead to the conclusion that the hypothesis of successive colonization of the western Pacific localities from sites in the eastern Pacific (or vice versa) by the planktonic larvae can be excluded. *Bathymodiolus thermophilus* is much more distinct from the western Pacific species than those are from each other.

The Atlantic *B.* ***puteoserpentis*** (and also the material from Barbados currently under study) has much closer affinity to the two western Pacific species than to *B. thermophilus*. If we assume that the inner mantle fold fusion is an apomorphic character and the absence of this fusion is plesiomorphic, it could be presumed that after the closure of the Isthmus of Panama, the eastern Pacific populations developed divergently from the remaining populations on the other side of the Isthmus, which remained more stable, as did the western Pacific populations.

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